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On the Reparative Processes which occur in Vegetable Tissues.

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IT may be right to state that the following observations were made without any knowledge that investigations of a similar kind had been in progress at the hands of others. Quite recently (September 1880) the work of Dr. Frank, 'Die Krankheiten der Pflanzen,' has been published; and this, amongst other subjects, contains an article on Repair. And to these observations I will refer, as occasion arises, in confirmation of, or as supplementary to, what is here recorded.*

I may pass over the effects which ensue after the amputation of parts in the simpler forms of vegetable tissues, as in septate Algæ, or those organisms (as *Ulva*) in which the component

* Sir James Paget has also referred to some of these in his address on Elemental Pathology, delivered at the Pathological Section of the British Medical Association, 1880.

cells are so arranged as to form a compact leaf-like parenchyma. The repair in all such simple cellular or parenchymatous plants, with perhaps very rare exceptions, is effected by disintegration of the cells spoiled and the unmodified growth of the parts immediately beneath. Frank * quotes from Hanstein a proper cell-repair as occurring in *Vaucheria*, the divided protoplasm of the thallus producing a cellulose partition continuous with the original wall, and the thallus subsequently growing out by the side of this terminal partition.

When it is considered, however, that the protoplasm in *Vaucheria* is polynucleated, this apparent exception is rendered perhaps conformable to rule; and I may proceed at once to consider the reparative processes as they occur in the higher plants. And as the tissues of these differ in no essential respects, I shall limit myself to phanerogamous plants, and even further, chiefly to those which are exogenous.

The subject of repair may be considered as it occurs, first, after *amputation*; secondly, after *incision*; and, thirdly, as it occurs in the *artificial union* of parts in grafting and budding. And under each of these headings the process may be noted, so far as necessary, as it proceeds in the stem, in the leaves, or in the root.

First, then, in regard to amputation. If the growing peduncle of the Hyacinth (*Hyacinthus orientalis*, Linn.), be half cut across, the growth of the parts proceeds without manifest interruption, and the divided surfaces appear at the termination of growth scarcely altered. A longitudinal section, when placed beneath the microscope, displays the divided cells scarcely displaced, empty, yet preserving their form, and still bounding the chief part of the surface. The cells beneath those spoiled are rounded at those ends which are towards the wound, whilst their opposite ends are flat and adapted to the flattened ends of the adjoining elongated cells, as the ends of these cells are adapted to one another. Besides this, the ends of some of the entire cells may be found enlarged, bulbous, or clavate; and some may have pushed bud-like processes from the sides of their enlarged extremities. The changes apply equally to the medulla and to the cortical parenchyma. The divided fibro-vascular bundles are overlapped by the overgrown bulbous and divided cells †.

* 'Die Krankheiten der Pflanzen,' p. 97.

† Frank notices a similar mode of repair from the mesophyll in the leaves of *Leucojum vernum*.

If the plumule be amputated in the Bean-plant (*Faba vulgaris*, Mill.), the axis is reproduced by an adventitious bud; and the divided surface, if the plant be grown in the warm moist atmosphere of a greenhouse, is repaired in much the same manner, the new surface being formed by a layer of elliptical loosely arranged cells.

On submitting sections of either to the action, first, of iodine solution, and afterwards of sulphuric acid, they stain throughout of a deep blue. In neither case does there occur any formation of cork in the surface of the injury.

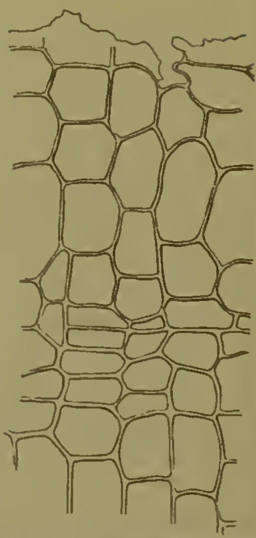
Frank observes, in the note before cited, that the new cells are indestructible by sulphuric acid, and are in this chemically different from the general parenchyma and resemble cork. But the repair in the case observed by him may have occurred under different conditions, since excess of moisture prevents the formation of cork, which is most readily produced in moderate dryness. In cases where the parts contain an abundance of sap, the process is modified by the formation of a scab of dry sap over the divided surface. For example, in *Ecbalium agreste*, on amputating a young leaf close to the growing procumbent stem, a copious flow of sap occurs from the vessels of the vascular bundles, and quickly forming a pellucid drop on the surface, dries as a firm glassy film through which the cut surface remains for some days clearly visible.

In the process of growth the layer of exuded sap is fissured, and the proper substance of the divided cells becomes exposed in its place. If the removal be made quite early, and the parts be examined microscopically some weeks afterwards, scarcely any change may be found to have occurred in the elongated parenchyma which forms the chief parts of such herbaceous stems and their subdivisions. Several layers of cells beneath the divided surface appear to be sharply outlined, and markedly different from the substance of the general parenchyma; but except at the very surface, these altered cells preserve their natural form. Beneath this encrusting layer, the cells may in some cases be found in certain spots less elongated, approaching to a flattened form; and in other cases, where the parts are allowed to attain full maturity, the living elongated cells have undergone oft-repeated divisions, so as thickly to cover the general tissue with cork and flattened subjacent phellogen.

But before such a new formation has had time to occur, the

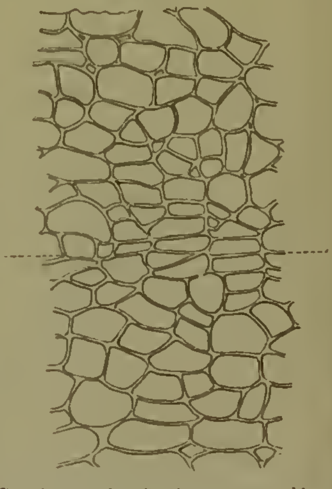
living parts, subjected to ordinary exposure, come to be nevertheless protected. I have noticed that in the earlier stages (such as may be seen fourteen days after the injury) the only change shown by the microscope will be that several tiers of the original elongated cells beneath the divided surface appear sharper in outline than those of the general substance, the altered layer being of uniform thickness and well defined from the rest of the parenchyma beneath, in which there may be in spots evidences of transverse partitioning. That the layer of altered cells has acquired new characters is shown by treating the section with iodine and sulphuric acid: whilst the general parenchyma is stained deep blue, these layers of surface-cells remain uncoloured, their walls having undergone a protective suberous change, though their elongated form shows these cells to be original elements of the petiole. This chemical change in the outer components of what is in its origin a single structure, may be compared in animal textures with the change in the outer cells of the cuticle, which are horny and not colourable with logwood, whilst those more deeply seated are wholly, or in part, of different composition and readily stained.

Fig. 1.



Section of *Ecbalium agreste*. Amputation through base of young petiole, repair after fourteen days, showing partitioning of the cells a short way beneath the surface.

Fig. 2.



Section of *Datisca cannabina*. Amputation through base of young petiole, repair after six weeks. Above the dotted line the tissue is suberous, the more superficial cells being unchanged in form, the deeper subdivided.

Similar changes are observable in the stems of *Datisca cannabina*, in the surfaces made by removing the portions which support the growing leaves. A thick layer of cork is formed of the original cells, most of which undergo subdivision to the second or third degree, forming short tiers of cells irregularly packed

together, and resting on a flattened subjacent phellogen; and similar ones are observable in the Hollyhock; and they may be assumed to be general in plants of the same longevity and like construction.

I have seen no proper cicatricial formation of cork in the Bean (*Faba vulgaris*, Mill.), whether grown under ordinary exposure or under the protective conditions of warmth and moisture. And it is perhaps true, generally, that the stems of herbaceous plants which last only one season, and in which no provision for leaf-fall exists, are incapable of such reparative process.

Indeed, in the Bean, when grown under the usual conditions, I have seen no change whatever in the parenchyma,—at the most a lesser readiness of the cells beneath the surface to react under the iodine and sulphuric-acid test; but even this change is irregular and undefined. Frank also notices this absence of repair in the same plant. He speaks, however, of an outgrowth of cells or callus from the cambium. I have observed such an outgrowth from the pericambium after amputation of the young root, but have seen no repair of an allied kind after removal of the stem, either in this or any other annual.

In *Ecbalium*, after amputation through the base of the young leaf-stalk, the ends of the fibro-vascular bundles killed in the division are raised from the deeper parts by the cell-multiplication. The spirals of the vessels may be found unrolled by the partitioning increase around, and stretched between the effete and the natural parts. In this way, by lateral compression, attenuation, perhaps rupture, the vessels are permanently closed beneath the temporary crust of sap.

Leaving the effects of amputation in trees for later consideration, the case may be next considered of those plants which are intermediate in structure and longevity between herbaceous annuals and exogenous trees. One of the most convenient to take is the common so-called Geranium, *Pelargonium* sp.

If a branch be removed near the parent stem, the cells injured by the division, together with several layers of those beneath, wither, and form a tough buff-coloured membranous layer, beneath which the growth of the living parts uninterruptedly proceeds. The process of growth being maintained in the subjacent parts, the inextensible incrusting substance becomes cracked, and its fragments disparted and loosened from the growing parts beneath,

so as finally to be completely separated. The surface will then appear silver-grey, dry, shining, and membranous; and contrasting with the earlier stages, both the ground-substance of the cortex and the pith are slightly convex, the zone of dead wood and bast being hidden in the furrow between. The new surface resembles in all its characters the general surface of the stem; and a microscopic section shows the central and peripheral parenchyma to be invested with a uniform layer of flattened suberous cells, closely arranged in tiers and set in rows on the subjacent surface. The new layer is continuous at the margin with the deeper part of the periderm.

The same steps of cork-formation may be here observed as were before noticed. A section treated with iodine and sulphuric acid will show, forming the actual surface, a crust of the original unaltered cells, dead, stained blue (as dead cellulose is), and still crammed with starch; beneath this the elements cease to give the cellulose reaction; and the cells are traceable in various phases of cross-multiplication, from the simplest most outwardly, with increasing degree and regularity, till the dividing parenchyma has produced a considerable thickness of tabular corky cells resting on an ordinary phellogen, the cells of which pass by gradations into the general parenchyma.

This is the ordinary mode of repair. But there may be added a formation of sclerenchymatous tissue in the pith a short distance beneath the flattened growth of cork described, the ground-tissue of the pith producing secondary meristem of elongated cells set across the axis of the amputated branch, the deeper of which cells undergo thickening and conversion into woody parenchyma. The medulla in such a case is closed by a dome of hardened tissue continued into the wood at its margin. The process recalls the closing of the medullary canal of the bone in an amputation-stump by new osseous tissue. The cap of new bone in such circumstances may be formed in the substance of the granulations which grow from the exposed medulla, though at other times it is produced in an intermediate fibrous membrane; and in the case which I have described the sclerosed tissue is formed of the indifferent cells of the pith and those to which these cells give rise.

Somewhat similar results are observable after the removal of branches in *Aucuba japonica* and the fleshy stems of Cactaceæ.

In *Cereus* the surface of an amputation is repaired as follows:—

Supposing the tissue to have been treated with iodine and sulphuric acid, a section will display on the general parenchyma a blue-stained phellogen, succeeded by flattened unstained cells of cork and a line of red or yellow sclerenchyma, two, three, or even four cells deep, these sclerotic cells being ranged in order with the flatter cork, and themselves succeeded by flattened suberous cells like those which lie beneath them; on the cork are larger cubical or spheroidal cells, the deeper unstained, those of the surface dead aud deeply coloured blue.

Injuries of amputation in *Opuntia* are healed in a similar manner, a partition of sclerenchyma being formed so as to lie in the midst of the flattened corky layer. The thickening affects first the outer wall of the cell; and in later stages the outer walls of the cells, or those towards the surface, are often thickened in excess of those opposite. Yet this particular mode of repair is not so general in the Cactaceæ that it may be deemed a rule. In *Mammillaria*, for instanee, repair is effected by tiers of tabular cork and phellogen without the formation of sclerenchyma.

The relationship which the new-formed cells bear to those of the general surface may appear, also, in the nature of their contents. Thus iu the stems of *Cacalia articulata*, where the cells for two or three rows beneath the epidermis are flattened and hold cubical or rhomboidal crystals, the flattened cells of the repair beneath the cork coutain similar crystals, whilst there are none such in the cortical parenchyma or in the cells of the pith.

It is interesting to observe, as showiug some similarity to the reparative proeess as it occurs iu Mammalia, that the cicatricial tissue does not acquire the full structure of that which it laces. The new tissue is devoid of stomata, which on the stems of Cactaceæ are abundant; nor are such ever formed in, nor hairs upon it; as in animal sears, there are produced no sweat-glands or hair-follicles.

It is worthy of note also that the new covering does not spread from the edges of the original investment, but that its formation occurs simultaneously at all parts of the injured surface.

Now this process of healing is, in essential respects, parallel with the healing beneath a scab as it occurs in animal tissues—the form of healing which is most eommon in animals, and the general mode of the healing of open wounds iu vegetable

tissues. But the spread of an epidermis from the margin of the wound, which occurs in animal tissues in the process of scabbing, does not take place in plants. No such lateral growth is observable after a partial removal of epidermis, whether the parts be left unprotected or kept beneath a bell-jar in an atmosphere saturated with moisture. In the latter case the cells exposed may preserve their vitality. After the removal of epidermis from the leaves of the Hyacinth, I have seen some of the denuded vertical cells elongated and club-shaped, as after partial section of the peduncle.

In *Agave* a many-layered covering of cork is produced on that portion of a leaf from which the original epidermis has been removed; and the same is true of succulent leaves, the repair being the same as that set up after the injury of an amputation.